AN APPARENT OVEREXPLOITED LYNX POPULATION ON THE KENAI PENINSULA, ALASKA

THEODORE N. BAILEY, Kenai National Wildlife Refuge, Box 2139, Soldotna, AK 99669
EDWARD E. BANGS, Kenai National Wildlife Refuge, Box 2139, Soldotna, AK 99669
MARY F. PORTNER, Kenai National Wildlife Refuge, Box 2139, Soldotna, AK 99669
JOHN C. MALLOY,[1] Kenai National Wildlife Refuge, Box 2139, Soldotna, AK 99669
RICHARD J. McAVINCHEY,[2] Kenai National Wildlife Refuge, Box 2139, Soldotna, AK 99669

Abstract: Available data suggest that lynx (*Felis lynx*) were overexploited during the last decade on the 7,972-km² Kenai National Wildlife Refuge (KNWR), especially in its accessible portions. Lynx harvest during the anticipated peak population (1983–84) was >80% below that of the last peak (1973–74) despite increased trapping effort, adequate habitat, and abundant prey. The majority (66%) of lynx taken from 1977–84 came from remote habitats rather than accessible, prey-abundant habitats. Radio-collared lynx mortality, primarily from trapping, increased from 41 to 86% between 2 trapping seasons (1982–83 and 1983–84) and totaled 90% during 649 days (1982–84). Mortality rates were higher for adult males (88%) than adult females (45%). Two radio-collared adult females with young used 50- and 89-km² areas while 2 adult males used 64- and 783-km² areas. Lowland (129 m) forest in a 1947-burned area and upland (346 m) transitional habitats were utilized by lynx. Estimated snowshoe hare (*Lepus americanus*) densities were as high as 1,233/km² in a 1947-burned forest during 1983 and 1984. Low lynx numbers and harvest and other data, despite abundant habitat and prey, indicated a depressed lynx population. Management implications and actions taken are discussed.

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Recruitment into lynx populations is extremely low or lacking for ≥3–4 years after snowshoe hare populations crash (Nellis et al. 1972, Brand and Keith 1979, Parker et al. 1983) because of reduced productivity and high kitten mortality. Lynx also are highly susceptible to trapping (Mech 1980, Carbyn and Patriquin 1983, Parker et al. 1983), and trapping mortality appears additive to natural mortality (Brand and Keith 1979). These factors make lynx populations prone to overexploitation.

Overexploitation was assumed responsible for successively lower lynx population peaks across Canada in 1925–26, 1935–36, and 1944–45 (de Vos and Matel 1952). Butler (1942) believed lynx in western Canada were limited by trapping rather than food supplies. Keith (1963) reported a scarcity of lynx in central Alberta and Saskatchewan and southern Manitoba between 1958 and 1963 despite high hare numbers. Fox (1978) also believed that lynx were overexploited between 1929 and 1954 in Canada. Berrie (1974) speculated the decreasing amplitude of the lynx cycle in Alaska also was due to overexploitation.

The rapid increase and persistent high value of lynx pelts since the mid-1970's generated a great demand for lynx fur. The apparent poor response of lynx populations to increasing snowshoe hare numbers on the KNWR, Alaska, as reflected in the harvest and scarcity of tracks in areas formerly used by lynx, prompted this investigation. The objectives were to document harvest, mortality, and movement patterns of lynx; estimate their numbers; and determine the relative and absolute abundance of snowshoe hares, the principal prey of lynx.

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STUDY AREA

The 7,972-km² KNWR is situated on the Kenai Peninsula (26,000 km²) in southcentral

[1] Present address: P.O. Box 2933, Missoula, MT 59806.

[2] Present address: Walsh Hall, Apt. 12, University of Alaska, Fairbanks, AK 99701.

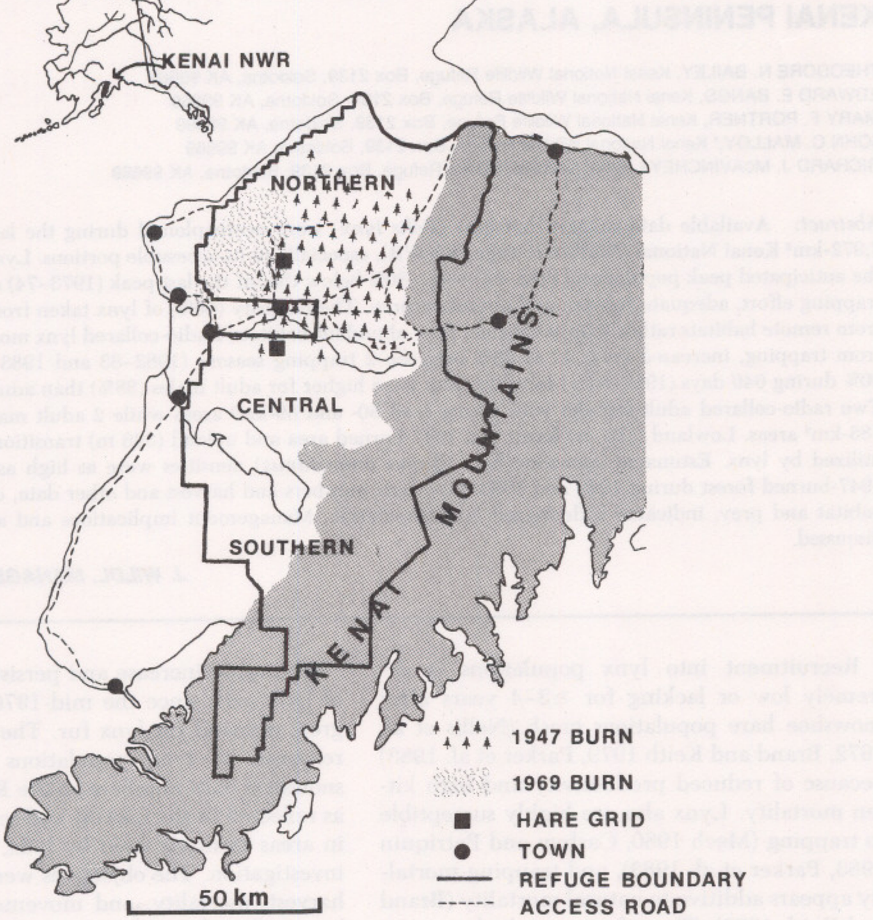

Fig. 1. Kenai Peninsula and location of the Kenai National Wildlife Refuge, Alaska. Dark area is mountainous and light area is lowlands.

Alaska. ADFG Game Management units 7 and 15 occur within the KNWR, and unit 15 is subdivided into 15A, 15B, and 15C. These subunits include the northern, central, and southern regions of the KNWR, respectively (Fig. 1).

Three major topographic features characterize the KNWR: the eastern Kenai Mountains rising to 1,600 m, the Skilak-Tustumena benchlands which average 823 m, and the western lowlands averaging about 122 m. The lowlands and forested mountainous slopes ≤500 m are dominated by white (*Picea glauca*) and black spruce (*P. mariana*), paper birch (*Betula papyrifera*), willow (*Salix* spp.), and quaking aspen (*Populus tremuloides*). Two major wildfires within the northern region of the KNWR, one burning 898 km² in 1947 and another 303 km² in 1969, provided forest successional habitat.

LANDSAT-derived habitat information (T. N. Bailey, unpubl. rep., U.S. Fish and Wildl. Serv., Anchorage, Alaska, 1984) indicated the majority of habitat for lynx on the KNWR occurs in forests (3,370 km²) and the remainder (1,308 km²) in nonforested subalpine, montane, and lowland shrubs or shrub-dominated wetlands and bogs. Lakes, open alpine areas, permanent snow, ice, glaciers, mudflats, gravel outwash, and rock were not considered lynx habitat. Two general habitats appeared important to snowshoe hares and lynx. Most occurred at low elevation ($\bar{x}$ = 122 m) within successional forest in the northern region of the KNWR, and a Sitka alder (*Alnus sinuata*)-dominated subalpine shrub zone provided high elevation (300–400 m) habitat along the western face of the Kenai Mountains.

Most of our information was collected in the northern region of the KNWR where there are >3,000 lakes and ponds, 1,000 km of oil seismic exploration trails, and >100 km of roads. This entire northern area is open and accessible to trappers using aircraft, snowmobiles, and dog teams. Access is more difficult in the central region and is most difficult in the southern region of the refuge because of the scarcity of lakes and trails. Almost all lynx taken on the KNWR came from the northern and central regions.

TRAPPING REGULATIONS

Lynx trapping on the KNWR has been liberal. There have been no restrictions on numbers of trappers since 1967 or limits on numbers of traps, types or locations of sets, and numbers of lynx taken. No areas on the KNWR have been closed to trapping. From 1960 to 1982 a 4.5-month season from 15 November to 31 March was in effect. This was reduced by 15 days (to 15 Mar) during the 1982–83 season.

Trappers on the KNWR are required to have a free permit, permits have been unlimited, and trappers must file a harvest report. Prior to 1977, only total furbearer harvest from the KNWR was reported. Thereafter, information on the date, location of capture, sex, and estimated age of furbearers was reported. Because some trappers fail to obtain permits or file reports, the harvest data on lynx is considered minimal. However, since 1977, periodic cross checks indicate only a minor difference in reported harvest and pelts sealed by the ADFG.

METHODS

Lynx Movements and Mortality

Lynx were livecaptured by cooperating trappers on the KNWR during the 1982–83 and 1983–84 trapping seasons, immobilized, examined, and released if not seriously injured. Trappers were compensated for each released lynx at current pelt values. Twelve of 20 examined lynx were weighed, fitted with a 300-g radio collar, released, and aerially located 1–10 times/month until the lynx died or radio contact was lost. The area used by a lynx was defined by a line connecting the outermost relocation points. Mortality rates of radio-collared lynx were calculated as described by Trent and Rongstad (1974). Lynx carcasses were purchased from trappers between 1977 and 1984. Ages were determined by tooth development (Saunders 1964) and annuli in cementum layers of canine teeth (Nava 1970).

Snowshoe Hare Habitat Relationships and Densities

Snowshoe hare habitat relationships and densities were determined by hare pellet counts and marking and recapture of hares in 2 study grids, respectively. Nineteen single-sample pellet transects were distributed throughout the KNWR and adjacent Chugach National Forest between 13 September and 21 October 1983 and 14–17 June 1984. All but 1 transect consisted of 32 1-m^2 sample plots using a square plot frame. Sample plots were spaced approximately 9 m apart, 8/line, along 4 lines radiating in the 4 cardinal directions from a central, randomly selected point. All pellets in each 1-m^2 plot were counted. Permanent pellet plots were established at each of the 49 plot centers on the 3 permanent snowshoe hare grids. Hare pellets within the frame were counted and removed from the plots in 1983 and recounted between 24 May and 27 July 1984.

Snowshoe hares were livetrapped on 2 of 3 permanent grids located within the 1947-burned area using the methods of Wolff (1982). Double-door, cage-type live traps (23 × 23 × 81 cm) were arranged in a 7 × 7 grid, spaced 60 m apart, and set within 5 m of the plot center. A 3rd grid, where hares were not trapped, was in the 1969-burned area. Live traps usually were placed in well used hare runways, covered with natural materials, and baited with alfalfa cubes. Captured hares were eartagged with either size 1 or 3 No. 1005 monel metal ear tags (Natl. Band and Tag Co., Newport, Ky.) and aged as adults or young-of-the-year on the basis of genital morphology and body weight (Trapp 1962, Keith et al. 1968). Program CAPTURE (White et al. 1982) provided adult population and density estimates. The ratio of juveniles:adult in late August or September was taken as a conservative estimate of the number of juveniles alive:adult at the end of the breeding season. This ratio then was applied to the estimates of adult densities in the grid trapped earlier, before most juveniles were born, for a total population estimate.

Woody vegetation at each of 147 grid points was surveyed using the point-centered quarter

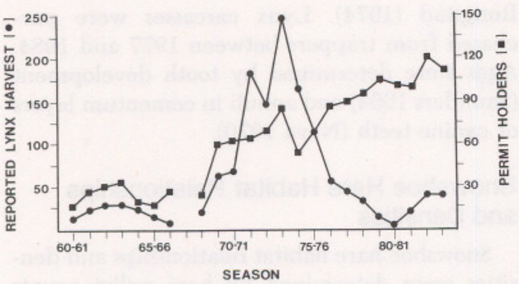

Fig. 2. Lynx harvest and number of trapping permits issued on the Kenai National Wildlife Refuge, Alaska, 1960–81.

method (Cottam and Curtis 1956). For the 4 woody shrubs at each plot the percentage of available twigs grown in 1982 and the percentage of all available stem endings browsed by hares were recorded. The diameters at point of browsing (DPB) were measured, and all growth <2 m aboveground, if not browsed by moose (*Alces alces*), was considered to be available to hares. At each plot the percentage of overhead cover >1 m aboveground was estimated (James and Shugart 1970).

RESULTS AND DISCUSSION

Lynx Harvest

After relatively little trapping of lynx in the early 1960's when their pelt prices were low, lynx harvest dramatically increased on the KNWR in response to increasing pelt values during the late 1960's and early 1970's. Harvest peaked at 245 during 1973–74 (Fig. 2) and coincided with peak snowshoe hare numbers (Oldemeyer 1983) rather than lagging 2 years behind as predicted by Brand and Keith (1979). Lynx harvest remained high after the snowshoe hares crashed (1974–75 = 162 and 1975–76 = 113). Harvest was only 38 in 1983–84, 10 years after the previous peak. Two years prior to the 1973–74 peak harvest total harvest was 327 lynx. Two years prior to the 1983–84 season the harvest was only 58 lynx. Even if the peak population occurs during 1985–86, the 1983–84 harvest is still 79% lower than that 2 years prior to the last peak.

The current lynx harvest also is low despite an increase in trapping pressure on the KNWR. Between 1971 and 1974, when lynx numbers were increasing during the last cycle, 207 KNWR trapping permits were issued. Between 1981 and 1984, during the current cycle, 340 permits were issued, an increase of 64%. The average number of lynx reported/permit holder declined from 3.0, 2.2, and 3.0 during 1971–72, 1972–73, and 1973–74, respectively, to 0.2, 0.3, and 0.3 during 1981–82, 1982–83, and 1983–84, respectively. Even if only permit holders that actually trapped were considered, the same trend occurs but with a slightly higher harvest rate/active trapper. Regardless of the comparison used, more trappers took significantly fewer lynx during 1981–84 compared to 1971–74.

The accessible northern part of the KNWR attracted most (71–86%) of the trappers and, therefore, received most of the trapping pressure. A minimum of 177,684 trap days was expended for all furbearers on the KNWR during the 1982–83 season, 53–64% of which were in the accessible northern region. Successful lynx trappers during the same season expended ≥85,250 trap days of effort (not all necessarily for lynx), 52,450 (61%) of which were estimated to occur in the northern refuge. Successful KNWR lynx trappers during 1982–83 had 20–150 sets out for 40–151 days and a success rate of 1,894 trap days/lynx capture (45 captured and 9 released). Successful lynx trappers had about 580 and 260 sets for all furbearers in the northern and central regions of the KNWR, respectively, during 1982–83. The number of sets made for lynx only was unknown because 70% of the trappers are opportunistic and trap for all species of furbearers (Bailey 1981).

The distribution of lynx harvest on the KNWR between 1977–78 and 1983–84, when snowshoe hares were increasing, revealed more lynx were taken from the central than northern region of the KNWR (Table 1) despite the central region's smaller size and lower quality (less early successional forest) lynx habitat and approximately 50% less trapping effort. Furthermore, the most successful lynx trapper in the central refuge did not trap lynx for 3 years (1979–82) in his exclusively used area when lynx population levels were low. There also was less trapline overlap in the central region.

Between 1977 and 1984, most lynx (66%) were taken in areas ≥4 km from the nearest maintained public road. Another 26% were taken in areas within 2–4 km of maintained roads or unmaintained roads open to snowmobile use. No more than 7 lynx/year were taken adjacent (<2 km) to roads between 1977 and 1984. The 2 oldest lynx trapped, both males, came from remote regions of the KNWR. A 12-year-old

Table 1. Distribution of lynx harvest within the Kenai National Wildlife Refuge, Alaska, 1977–84.

Region	Season							
	1977–78	1978–79	1979–80	1980–81	1981–82	1982–83	1983–84	Total
Northern	9	9	7	2	18	21	16[a]	82
Central	26	24	5	0	2	17[b]	22[c]	96
Unknown	7	0	0	0	0	3	0	10
Total	42	33	12	2	20	41	38	188

[a] Includes 3 radio-collared lynx released in 1982–83 and 1 in 1983–84.
[b] Includes 1 radio-collared lynx released in 1982–83.
[c] Includes 1 radio-collared lynx released in 1982–83.

male was trapped adjacent to a rugged, mountainous area >7 km from the nearest road in the northern region of the KNWR, and a 10-year-old male was taken in the central region >27 km from the nearest road. Females exceeded males in the reported harvest in 4 of 7 years between 1977 and 1983.

Lynx also were removed more rapidly in the northern than central regions of the refuge. The monthly distribution of captures of lynx between 1977 and 1984 differed ($P < 0.10$) with nearly 50% of the harvest on the northern refuge taken the 1st 52 days of the season. The proportion of lynx harvested in November in the northern refuge also increased from 5 to 28% between 1977–82 and 1982–84 but decreased from 28 to 15% in the central refuge. The 16-day shortening of the lynx season during 1983–84 did not reduce the number of lynx harvested in March in the northern refuge compared to the previous 6-year March average (1.0 lynx). Lynx harvest during March 1984 in the central refuge increased from a previous average of 1.6 to 4.0 lynx/month.

The average age of male lynx trapped in the northern and central regions of the KNWR after 1977 was 2.1 years ($N = 13$) and 1.8 years ($N = 17$), respectively. The average age of female lynx trapped from the same regions was 2.9 years ($N = 16$) and 1.6 years ($N = 15$), respectively. Their differences were not significant ($P > 0.05$), but few trapped males (10%) or females (29%) were >3 years old.

Lynx Mortality

The mortality rate of all radio-collared lynx during the 649-day monitoring period was 90%. Mortality rates nearly doubled between the 1982–83 (44%) and 1983–84 (86%) trapping seasons (Table 2). Mortality rates were lowest (0 and 29%) during nontrapping periods, and even then, deaths were believed to be trapping related. Mortality among juveniles was high (77%) over a relatively brief (125-day) monitoring period (Jan–May 1983) and nearly equivalent to that among adults (78%) for a monitoring period of >625 days. Lynx released prior to or during the 1983–84 season, or the offspring they produced, comprised 43% of the sealed 1983–84 lynx harvest in the northern region of the KNWR. Thus, the reduction in mortality of only a relatively few individuals was substantial over a vast area of the refuge.

Limited data are available on lynx mortality rates from other studies. Seasonal trapping mortality was estimated at between 8 and 30% in Alberta, averaging 10% of the fall population when lynx pelt prices averaged $44. It was between 17 and 29%, a 2–4-fold increase, when average pelt prices increased to $101 (Brand and Keith 1979). The maximum estimated mortality rate due to trapping was 42%, and

Table 2. Mortality rates of radio-collared lynx on the Kenai National Wildlife Refuge, Alaska, 1982–84.

Period or age of lynx	Days in period[a]	N: Lynx days[b]	N: Mortalities	Mortality rate during period[c]
Period				
1982–83 season	130	499	2	0.44
1983 offseason	223	1,311	2	0.29
1983–84 season	127	326	5	0.86
1984 offseason	169	350	0	0.00
Total	649	2,486	9	0.90
Age of lynx				
Adults[d]	649	2,141	5	0.78
Males	435	610	3	0.88
Females	458	1,531	2	0.45
Juveniles[e]	125	345	4	0.77

[a] As of 1 Sep 1984.
[b] Cumulative (N) of days live radio-collared lynx wore functioning radio collars.
[c] As per Trent and Rongstad (1974).
[d] 12 months old (assume juvenile lynx become adults on 1 Jun).
[e] ≤12 months old.

the maximum estimated mortality rates of kittens and adults during the 7-month nontrapping period were 95 and 38%, respectively.

The proportion of available lynx released in 1982–83 that was taken on the KNWR the following season (1983–84) suggested trapping was removing 80% of the individuals. Parker et al. (1983) reported that trapping removed 65% of his study population and that all marked lynx in a 60-km^2 area were killed by hunters and trappers within 1 year. Natural annual mortality of adults, excluding kittens but including yearlings, in a nonharvested area in Washington during a period of low prey abundance was <25% (J. D. Brittell, pers. commun.). Trapping mortality rates of KNWR lynx thus appeared 2–4× as great as reported elsewhere, and exceeded by 3× the adult mortality reported in an untrapped lynx population where natural mortality rates probably were high.

Trapping was the direct cause of mortality for 6 of 9 radio-collared lynx. Two of 3 other mortalities were juveniles that apparently died of starvation after adult females, assumed to be their mothers, were taken from the same areas. Although lacking direct evidence, it appeared that these kittens were unable to obtain sufficient prey without the help of the female. Another kitten released by a trapper died, presumably because of a leg injury but also after its mother was taken. Therefore, trapping related causes could have been responsible for all of the observed mortalities. Juveniles appear dependent on the female's hunting prowess throughout the winter, as suggested elsewhere (Saunders 1963, Brand et al. 1976, Parker 1981). We observed a family group together (lynx No. 7) in mid-January and observed tracks of other family groups in late March. Parker et al. (1983) suggested that orphaned young are very susceptible to trapping. No mortality from other causes (predation or disease) was recorded among radio-collared lynx or reported or observed from other lynx on the refuge between 1977 and 1984.

The areas used by radio-collared lynx, especially in the northern region of the KNWR, were intensively trapped. For example, ≥15 trappers operated within the oldest male lynx's area. His area was bisected by 2 gravel roads and >100 km of snowmobile and dog sled trails and contained ≥25 aircraft-accessible lakes. The other mature male's area was bisected by ≥2 traplines. Both males were taken by trappers within 1 year after their release. There were few areas the size of an area used by female lynx that were not trapped during the 1980's in the northern region of the KNWR.

Lynx were highly vulnerable to trapping. Juveniles appeared 5× as vulnerable to trapping as adults, and adult males were nearly 2× as vulnerable as adult females (Table 2). Juvenile vulnerability probably was related to family cohesiveness because harvest records commonly indicated several juveniles, presumably siblings, often were rapidly taken from a small area. Six of 7 radio-collared lynx were killed within 42 days of the opening of the trapping season or after they were released within the season. Four of these 6 lynx were taken during the following season after their release, and the average distance between the release and final capture site was 18 km (range = 0–29 km). Only 1 of the radio-collared lynx was taken by the same trapper in the same location. In Minnesota, when pelt prices were low, 7 of 14 radio-tagged lynx were killed by humans, and no natural mortality was documented (Mech 1980).

Lynx Movements

The areas used by 2 adult females with young in 1983 were 51 and 89 km^2. Areas utilized in the summer (25 km^2) by the adult females averaged less than winter areas (49 km^2). An adult male, monitored for 1 year, wandered extensively over 783 km^2 in the northern region of the KNWR and was found together with, or near, 2 widely separated radio-collared adult females during the 1983 breeding season. Another mature male, monitored only 42 days, used ≥64 km^2 before he was killed, and a juvenile male used an 8.3-km^2 area in the 1947-burned area before it dispersed. The terrain used by lowland residents averaged 129 m in elevation compared to 346 m for transitional-habitat residents.

During a period of high, increasing hare abundance in interior Alaska, an adult female and male lynx had home ranges of 13 and 25 km^2, respectively (Berrie 1974). During a period of low, declining hare numbers in Nova Scotia, an adult male and female had maximum (summer) home ranges of 25.6 and 32.3 km^2, respectively (Parker et al. 1983). In Minnesota female and male lynx had home ranges varying from 51–122 and 145–243 km^2, respectively, in an area with few lynx and numerous snowshoe hares (Mech 1980). Winter home ranges of female lynx with young in Alberta averaged 17.8 km², whereas those of adults traveling alone averaged 31.5 km² (Nellis et al. 1972). In Riding Mountain National Park, Manitoba, the home ranges of 2 females with kittens averaged 156 km², whereas that of a male was 221 km² during a period of increasing snowshoe hare density (Carbyn and Patriquin 1983). Although Nellis et al. (1972) were unable to demonstrate a significant relationship between lynx home range sizes and hare densities, the areas used by lynx we monitored were most comparable in size to those in the Minnesota and Manitoba areas with low lynx densities.

Lynx Numbers and Densities

Harvest data, movements of radio-collared lynx, visual observations of unmarked lynx associating with radio-collared lynx, and lynx tracks were used to estimate minimum numbers and densities of lynx in the northern and central regions of the KNWR. If the annual harvest rate was 80% of the lynx population as suggested by our mortality data, the highest estimated pretrapping population between 1977 and 1982 was 26 (1982) in the northern region of the KNWR, or 1.0 lynx/100 km² (Table 3). The highest estimated density of lynx in the high quality habitat in the 1947-burned area in the northern region of the KNWR was 2.3 lynx/100 km² in 1981. Locations of harvested lynx and movements, tracks, and observations of radio-collared lynx suggested that 23 and 20 lynx were present in the northern region and the 1947-burned area within that region of the KNWR, respectively, prior to the 1983–84 trapping season. This estimate was comparable to a Lincoln index estimate (20) based on the proportion of marked lynx available and captured prior to and during that season.

We also estimated potential lynx numbers on the KNWR between 1977 and 1982 and during 1983 by assuming lynx densities would have been similar to those documented at other areas where snowshoe hare densities were known and comparable to the KNWR hare densities (Table 3). These estimates suggested that lynx numbers estimated on the northern and central regions of the KNWR since 1977 were only 7–15% and 38–79%, respectively, of lynx numbers documented with comparable snowshoe hare densities. Estimated numbers of lynx on the KNWR since 1977 were most comparable with those associated with low rather than high snowshoe hare densities (Brand et al. 1976).

Table 3. Estimated numbers of lynx in the northern and central regions of the Kenai National Wildlife Refuge, Alaska, 1977–83.

Region of refuge	Estimated N of lynx: Highest between 1977 and 1982[a]	Estimated N of lynx: 1983[b]	Range of potential lynx N assuming the following lynx/100 km²: 20[c]	10[d]	3[e]
Northern[f]	26	23	344	172	52
1947 burn[g]	19	20	161	81	24
Central[h]	32	34	85	43	13

[a] Based on a harvest rate of 80% of population, as suggested by the harvest of available radio-collared lynx during the 1983–84 season.
[b] Based on radio-collared lynx, tracks, visual observations, and harvest.
[c] From Parker et al. (1983) when hare densities were 1,000/km².
[d] From Brand et al. (1976) when hare densities were 499/km².
[e] From Brand et al. (1976) when hare densities were 34/km².
[f] Area = 2,465 km² for estimated numbers and 1,721 km² for potential numbers.
[g] Area = 807 km².
[h] Area = 1,362 km² for estimated numbers and 426 km² for potential numbers.

That the refuge supported high densities of lynx during the previous (1973–74) peak is suggested from previous harvest. One trapper took 18 lynx in a road-accessible area (Skilak Loop) during 1970–71, before the peak, for a harvest density of 10 lynx/100 km²; 2 trappers took 26 lynx from a 155-km² area in 1974–75, after the peak, for a harvest density of 17 lynx/100 km². Although the role of social behavior is unknown in determining upper lynx densities, this suggests that lynx densities were ≥10 lynx/100 km² and possibly >20 lynx/100 km² on the KNWR during the previous peak population.

Snowshoe Hares

Snowshoe hare populations previously peaked on the KNWR in 1973–74 (Oldemeyer 1983) and remained low until about 1978 when they began to increase noticeably. Observations prior to our study suggested that hares were extremely abundant in the 1947-burned area since 1981. Single-sample pellet surveys in 1983 indicated highest snowshoe hare use, and presumably winter densities, in the 1947-burned area, with considerably less use of the alder-dominated and 1969-burned habitats, and lowest use of the mature forest (Table 4). Pellet densities in the 1947-burned area in 1983 and in the

Table 4. Average snowshoe hare pellet densities by lynx habitat type on the Kenai National Wildlife Refuge, Alaska, 1983–84.

	1983						1984					
	Single samples			Permanent plots			Single samples			Permanent plots		
Habitat type	$\bar{x}$	N	SD	$\bar{x}$	N	SD	$\bar{x}$	N	SD	$\bar{x}$	N	SD
Forested												
Mature forest	7.9	128	18.1									
1947 burn	94.5	180	74.4	55.0	49	49.9				42.1	98	33.7
1969 burn	21.0	128	32.7	64.3	49	72.4	115.4	64	107.3	109.5	49	105.5
Nonforested	29.1	128	107.9									

permanent grids in 1984 were much higher than those reported by Wolff (1980) or Parker (1981) at hare densities of 590–1,000/km², respectively. Although comparisons are difficult because of the methods used and unknown pellet decomposition rates, average snowshoe hare pellet densities recorded in the 1947-burned area in 1983 ($N = 278$, $\bar{x} = 81.5/m^2$) exceeded those reported from other studies (MacLulich 1937, Adams 1959, Dolbeer and Clark 1975, Wolff 1980, Orr and Dodds 1982) with the exception of a cyclic peak in West Virginia (Brooks 1955).

Snowshoe hare densities in the 1947-burned area in 1983 exceeded 1,000 and 300/km² in grids 1 and 3, respectively. In 1984, densities were >1,200 and 400/km² in Grids 1 and 3, respectively (Table 5). Capture success, which paralleled density estimates, suggested a slightly increasing density of hares in Grid 1 and a stable or slightly declining density in Grid 3. Overhead cover, an important component of snowshoe hare habitat (Wolff 1980) was not different ($P > 0.05$) between Grid 1 (19.4%) and Grid 3 (12.8%). Other studies (Ernst 1974, Keith and Windberg 1978, Wolff 1980, Parker et al. 1983) estimated densities of 400–2,291 hares/km² during population highs.

Hare browsing intensity in the grids also suggested that hares were at peak densities in 1983. The mean DPB for paper birch in grids 1 and 3 was 3.1 ($N = 67$) and 3.4 mm ($N = 74$), respectively, and for all browse species it was 2.5 mm. Because hares forced to consume twigs with a diameter >3 mm cannot maintain body weight through winter and thus starve (Pease et al. 1979), Wolff (1980) used a DPB of >3 mm as an indicator of food stress. Browsing intensities in the 1947-burned area in 1983 ranged from 75 to 87% for paper birch, 51 to 73% for willow, and 31 to 58% for aspen. Only 32% of the birch was browsed by hares in the 1969-burned area in 1983 compared to 42% in 1984. During 1973, when snowshoe hares on the KNWR were at their last peak, an average of 86% of all birch plants was browsed by hares in the 1947 burn near the Moose Research Center (Oldemeyer 1983). This was lower than the 100% browsing intensity reported by Wolff (1980) for a hare peak in interior Alaska.

The transitional vegetation zone between the forested and alpine habitats received only 33% of the hare use (29 pellets/m²) of that in the late successional forest (94 pellets/m²). Alder swamps and transitional zones between lowlands and uplands were important habitats for hares in Minnesota (Green and Evans 1940) and Michigan (Bookhout 1965). These remote habitats could serve as natural refuges for hares and lynx. Concentration of lynx sign in this zone on the refuge was reported 1st in the early 1950's (Kenai Natl. Moose Range, unpubl. rep., Kenai, Alaska, 1951). Upland refuges in valleys, which supported pockets of hares and lynx during hare lows, was postulated for interior Alaska by Berrie (1974). Wolff (1980) reported that willow-alder thickets provided refuges for hares especially from avian predators.

CONCLUSIONS

Although largely circumstantial, the magnitude of available data strongly suggests that the lynx population in the northern region and, to a lesser extent, in the central region of the KNWR was overexploited during 1973–83. By overexploitation we mean an intense, persistent, and prolonged harvest for >10 years that exceeded the capacity of the lynx population to compensate for natural and human mortality and to naturally fill in vacancies left by the removal of lynx in more accessible habitats. Intensive exploitation began in the early 1970's with the demand for lynx pelts and was enhanced by the relatively easy access of trappers into lynx habitat, especially into the northern region of the KNWR. We believe it depressed the population well below a level that naturally would have been determined by the food supply. Our conclusions are based on the following circumstantial evidence: (1) depressed harvest levels (a decline of >80%) at assumed comparable points during the last 2 lynx-hare cycles; (2) a peak lynx harvest that corresponded with peak snowshoe hare numbers instead of lagging 1–2 years behind; (3) intense trapping pressure and harvest distribution that indicated more lynx were taken in assumed poorer quality, remote habitats than higher quality, accessible habitats; (4) the scarcity of untrapped, natural refugia for lynx in the northern region of the KNWR; (5) a trend that suggested lynx were taken more rapidly in accessible habitats; (6) low lynx harvest and estimated numbers despite an abundance of snowshoe hares exceeding some of the highest reported densities; (7) the apparent capacity of mid-successional stage forest habitat to provide more harvest than occurred between 1977 and 1984; (8) the high trapping mortality of radio-collared lynx of all ages; (9) the lack of evidence of any other significant source of mortality; (10) large areas used by lynx in spite of high prey populations suggesting low lynx densities; and (11) estimated low population levels of lynx compared to previous and potential population levels.

The lynx population in the central region of the KNWR appeared less impacted by exploitation during this period despite its smaller size and lesser amount of early successional stage forest, which is favorable to snowshoe hares. This was probably because trapper access was more difficult and the area included untrapped, natural refugia. We believe the natural refugia in the central region of the KNWR supported low populations of adult lynx after the last snowshoe hare decline. When the hares increased natural recruitment of lynx was able to refill the vacancies resulting from trapping. However, because few lynx tracks were reported and lynx were harvested in the more accessible northwestern part of the central region, we believe trapping also had influenced lynx numbers there but to a lesser degree.

Hares were not believed to have been significantly more abundant during the 1973–74 peak than during 1983–84 for the following reasons: (1) hare densities probably were extremely low in the 1969-burned area during the 1970–74 period because of the lack of cover and food in the then 1–5-year-old burn; (2) there was probably less permanent overhead coniferous cover in the 1947-burned area during the 1973–74

Table 5. Snowshoe hare capture effort, success, and estimated densities on 2 360 × 360-m grids within the 1947-burned area on the Kenai National Wildlife Refuge, Alaska, 1983–84.

Grid no.	Year	Trap nights	Hares captured: Adults	Hares captured: Juvenile	Total captures	Hares/km²: A[a]	Hares/km²: B[b]
1	1983	686	23	11	64	1,102	1,026
	1984	784	33	20	85	1,233	
3	1983	784	27	76	232	304	532
	1984	833	47	79	216	509	482

[a] Estimate from most appropriate model selected by program CAPTURE.
[b] Estimate from 2nd most appropriate model selected by program CAPTURE. (See White et al. [1982] for a description of models.)

peak compared to 1983–84 because of successional changes; (3) hare browsing intensities generally were lower on the refuge during 1973 (Oldemeyer 1983) than reported in interior Alaska during a population peak which approached 600 hares/km² (Wolff 1980); and (4) the 1983 hare densities and pellet counts were among the highest reported. However, the capacity of burns to support high densities of snowshoe hares and lynx undoubtedly declines with time (Fox 1978).

Hares on the KNWR may maintain their current densities well into the future instead of following the classical 10-year cycle and thus give lynx an opportunity to increase another 1–5 years. An extended peak hare population may be possible, especially because mild winters with little snowfall are common on the Kenai Peninsula (Bangs and Bailey 1980), whereas cold temperatures and deep snow are correlated with low adult survival (Meslow and Keith 1971). However, present hare browsing intensities and DPB of stems in the 1947-burned area suggest that hares are near that habitat's carrying capacity. Therefore, we do not rule out another 1–2 years of high hare densities on the KNWR. But given the current mortality rates of lynx and their estimated low population levels relative to habitat and prey, we believe a 1–2 year delay in a hare population crash would not allow KNWR lynx populations sufficient time to recover to potential levels.

MANAGEMENT IMPLICATIONS

The effects of intensive exploitation on lynx populations will undoubtedly vary, among other factors, with the presence and size of natural, untrapped refugia. When trapping pressure increased during the last 10 years on the KNWR, areas which previously served as natural refugia for lynx because of difficult or controlled access were exploited by alternative modes of access. Areas closed or inaccessible to aircraft were exploited by trappers hiking on foot or using dog teams. Where snowmobiles were permitted, trappers extended traplines into remote areas by making new trails or using old oil and gas seismic exploration lines for trails. High lynx pelt prices provided the incentive to expend the extra effort and expenses to exploit these remote areas. As exploitation increased, fewer lynx were taken and less sign of lynx was observed in accessible areas. Because of these events, it was important to document changes in harvest distribution because few lynx were taken from vast areas of suitable habitat. However, with sustained exploitation lynx eventually were removed from the remaining refugia and harvest continued to decline.

The minimum size of refugia needed to maintain viable populations of lynx where they are cyclic and heavily exploited is unknown. Our data suggested that the majority of lynx were being removed from the nearly 2,500-km^2 northern region of the KNWR in the 10 years between 1973 and 1984. Under heavy exploitation $\geq$50%, perhaps 80%, of the lynx were removed annually from the most accessible areas. Had it not been for several rugged mountain valleys that supported lynx along the eastern flank of the KNWR, there may have been even fewer lynx in the harvest. We speculate that vacancies caused by initial exploitation in the lowlands were filled by lynx dispersing from refugia in the remote, mountainous area. However, as exploitation increased, trappers actively searched out remaining pockets of lynx in the mountains, began to impact these natural refugia, and influenced the flow of dispersing lynx into other areas of the northern region of the KNWR.

The minimum area required by individual lynx to survive periods of snowshoe hare scarcity is unknown. We suspect it is much larger than the areas we documented during periods of hare abundance. Resident bobcats (*F. rufus*) enlarged their areas of use or abandoned traditional home ranges after their staple prey declined (Bailey 1974). Therefore, areas required to maintain viable lynx populations during lows and with intensive trapping may be large compared to periods of hare abundance. For example, Carbyn and Patriquin (1983) believed trappers outside the park could extirpate lynx from the entire 2,944-km^2 Riding Mountain National Park because lynx home ranges were so large during periods of low hare abundance. The park was not large enough to sustain a viable lynx population and lynx had to be replenished from outside the park boundaries. Our observations on the northern region of the KNWR, which is of similar size, support that concern.

Fisher (*Martes pennanti*) are similar in many aspects (reproductive rate, population density, food habits, cyclic with snowshoe hares, and high vulnerability to trapping [Strickland et al. 1982]) to lynx. Models of fisher populations (Powell 1979) suggest that the mere removal of >1–4 individuals/100 km^2/year by trapping could cause local fisher extirpation, perhaps over much larger areas.

The intensive exploitation of lynx on the KNWR coincided with 3–5 years of low hare densities and presumed low or negative lynx population recruitment. Brand and Keith (1979) recommended at least a 3-year curtailment of trapping during lynx population declines to ensure survival of adequate breeding populations for the next cycle. A comparison of the KNWR lynx harvest during the increase phases of the last 2 lynx cycles indicated 576 fewer lynx were taken during the last cycle. At an average Seattle fur auction price of $301.30 (Mar 1984), the economic loss to KNWR trappers could have been as high as $173,550, which supports the rationale behind Brand and Keith's (1979) recommended lynx harvest strategy. Our data further suggest that in highly accessible areas with few natural refugia, curtailment of trapping up to 5 years may be necessary to protect viable breeding populations of lynx. Thereafter, quotas or highly shortened seasons will be necessary to prevent overexploitation. Future overexploitation is especially a concern considering that the average value of lynx pelts taken from the KNWR during 1984–85 exceeded $500/pelt.

Because of intensive exploitation, lynx trapping was closed in the northern region of the KNWR by an emergency order of the ADFG prior to the 1984–85 trapping season. Throughout the remainder of the Kenai Peninsula, including the KNWR, the lynx season was shortened to reduce harvest from 120 to 47 days. To reduce incidental catch of lynx on the remainder of the KNWR, cubby, bait, and flag sets for gray wolves (*Canis lupus*), coyotes (*Canis latrans*), and wolverine (*Gulo gulo*) were prohibited before and after the shortened lynx season and were prohibited entirely from the northern region of the KNWR. These management actions may have to remain in place for 3–5 years and hopefully will allow lynx populations, especially in the KNWR's northern region, to recover while snowshoe hares are still abundant. If successful, the lynx population should expand into unoccupied habitat and reach levels to ensure that adequate numbers are available after the hare's decline to respond to the next hare population increase. Efforts also are underway to develop a reliable and practical lynx census technique, to increase our knowledge of lynx ecology, and to adopt a new furbearer conservation plan for the KNWR.

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